Re-instatement of the name *Spyridium waterhousei* from Kangaroo Island, South Australia, with a short history of the tribe Pomaderreae (Rhamnaceae)

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Abstract

The name *Spyridium waterhousei* F.Muell. is re-instated for a species of Rhamnaceae (Pomaderreae), endemic to Kangaroo Island, South Australia, that is currently known as *Cryptandra waterhousei* (F.Muell.) F.Muell. The taxonomic history of the species and of the tribe Pomaderreae is explored and the changing generic concepts are reviewed in the light of recent publications. A lectotype is nominated for the species. It was named after Frederick G. Waterhouse, who was one of the first botanical collectors on the island.

Introduction

"[M]ost of the genera [of Australian Rhamnaceae], even the most natural ones, are difficult to characterize. The differences in their flowers and fruits are very trifling; they often pass into each other by the finest gradations, and habit, foliage, and inflorescence must often be relied upon for fixing generic limits."

George Bentham, Flora Australiensis 1: 410

Waterhouse and Kangaroo Island botany

Frederick George Waterhouse (1815-1898) was curator of the South Australian Institute Museum from 1860-1882 (Kraehenbuehl 1976). Early in 1861, he was sent on an expedition to Kangaroo Island by the South Australian Government, chiefly to collect zoological specimens, but he also gathered "as a result of byework about a hundred species of plants [...], which passed into the hands of Baron F. von Mueller" (Tate 1883, p. 133). His main collection grounds were along the Cygnet River near Kingscote in the northern part of the island. Mueller eagerly awaited the arrival of Waterhouse's collections, as he mentions them in several of his reports and letters (e.g., Mueller 1861a, b, c). On 5 March 1861, George Francis, director of the Adelaide Botanic Gardens, sent "the entire collection of plants and seeds brought by Mr Waterhouse from Kangaroo Island" to Mueller (Best 1986, p. 116).

Mueller must have worked on the collection during 1861 and 1862, in preparation for the first volume of *Flora Australiensis* (Bentham 1863), as he described and published many species to make the names available for George Bentham. Waterhouse's specimens added a substantial number of species to the flora list

of Kangaroo Island. Five taxa were new to science¹, and one of them, *Spyridium waterhousei*, was named by Mueller in honour of Frederick G. Waterhouse. The subsequent taxonomic history of the species reflects the confusion in the delimitation of the generic limits in Australian Rhamnaceae, in particular within the tribe Pomaderreae Reissek ex Endl.

The generic limits of Pomaderreae

Pomaderreae is the second largest tribe of Rhamnacae and is endemic to Australia and New Zealand. It contains about 90% of Rhamnaceae species in Australia (c. 220–230 species) and currently consists of seven genera: Blackallia C.A.Gardner, Cryptandra Sm., Pomaderris Labill., Siegfriedia C.A.Gardner, Spyridium Fenzl, Stenanthemum Reissek, and Trymalium Fenzl. In Australia it is mainly distributed throughout the southern, temperate and semi-arid regions, but some species occur in the arid centre and the tropical North of the continent. Only Pomaderris extends to New Zealand with eight species that mainly occur on the North Island (Kellermann et al. 2005).

The generic history is summarised in Table 1 and Figure 1. In the 18^{th} and 19^{th} century, eleven genera were published in Pomaderreae, including the five main genera that are still accepted today (*Cryptandra*,

Bertya rotundifolia F.Muell. (Euphorbiaceae), Petrophile multisecta F.Muell. (Proteaceae), Pimelea ligustrina var. macrostegia Benth. (= Pimelea macrostegia (Benth.) J.M. Black: Thymelaeaceae), Spyridium nitidum N.A. Wakef., and S. waterhousei F.Muell. (Rhamnaceae). Tate (1883, p. 133) mentions "five species new to science". As Spyridium nitidum had not yet been described in 1883, Tate must have included Spyridium leucophractum (Schltdl.) F.Muell. in his count; this, however, was only a new combination. Wakefield (1957) used Waterhouse's collection much later to describe S. nitidum.

Table 1. Genera of Pomaderreae and their taxonomic status, listed in order of publication. Currently accepted genera are indicated in bold type.

Year of publication	Genus	Type species	Species number/ Taxonomic status	
1798	Cryptandra Sm.	C. ericoides Sm.	c. 55 species	
1805	Pomaderris Labill.	P. elliptica Labill.	c. 75 species	
1819	Pomatoderris Schultes	not designated	nom. illeg. & superfl. = Pomaderris Labill.	
1824	Pomatiderris Kunth	not designated	nom. illeg. & superfl. = Pomaderris Labill.	
1837	Trymalium Fenzl	T. ledifolium Fenzl	c. 13 species	
1837	Spyridium Fenzl	S. eriocephalum Fenzl	c. 40-45 species	
1838	Ledelia Raf.	L. betulina (Hook.) Raf.	= Pomaderris Labill.	
1848	Wichuraea Nees ex Reissek	not designated	= Cryptandra Sm.	
1858	Stenanthemum Reissek	S. leucophractum (Schltdl.) Reissek	c. 30 species	
1858	Stenodiscus Reissek	S. ulicinum (Hook.) Reissek	= Spyridium Fenzl	
1891	Solenandra Kuntze	not designated	nom. illeg. non Hook.f.	
1934	Siegfriedia C.A.Gardner	S. darwinioides C.A.Gardner	1 species.	
1942	Blackallia C.A.Gardner	not designated	2 species (currently under review, see Kellerman et al. 2005)	

Pomaderris, Spyridium, Stenanthemum, Trymalium). The superfluous Pomatoderris was published presumably in an attempt by Schultes (in Roemer & Schultes 1817-1830) to correct Labillardière's spelling of the generic name Pomaderris. Possibly for the same reason, Kunth (1824) created the name Pomatiderris. Ledelia was created by Rafinesque (1838) for one species of Pomaderris, P. betulina. Wichuraea Nees ex Reissek and Stenodiscus Reissek were erected for species of Cryptandra and Spyridium respectively (Reissek 1848, 1858), and stem from an era in which the full extent of the variation within these genera was not yet fully understood. Ledelia, Wichuraea and Stenodiscus were not accepted by contemporary botanists of Rafinesque, Nees von Esenbeck and Reissek. In his quest to reform and standardise the 'Rules of Botanical Nomenclature', Kuntze (1891) published the superfluous Solenandra to replace Stenanthemum, since he was of the opinion that Cryptandra subgen. Solenandra Reissek should have retained its name when Reissek raised it to generic rank. By doing this, however, Kuntze created an illegitimate name due to the presence of an earlier homonym, Solenandra Hook.f. (Rubiaceae). Two genera were added to the tribe Pomaderreae in the first half of the 20th century by Gardner (1933; 1942) for Western Australian endemic species, Siegfriedia and Blackallia. The latter genus was not typified and recent analyses have shown that it consists of two unrelated species (Kellermann et al. 2005); a review of Blackallia is in progress. The analysis of Kellermann et al. (2005) also indicated that at least two new genera would be necessary to accommodate some unique species from Western Australia and Queensland. These will be published in the near future (Kellermann et al., in press & in prep.).

The first synopsis of Australian Rhamnaceae was published by Fenzl in 1837, in a five page long footnote in *Enumeratio plantarum [...] Hügel*. This was followed by a summary of Western Australian species by Reissek (1848) and a treatment of the family for *Plantae Muellerianae* (Reissek 1858). Both authors were experts of Rhamnaceae and defined some of the main genera of Pomaderreae (Fig. 1).

When writing the *Flora Tasmaniae*, Joseph Dalton Hooker "had great difficulty in disposing the species of the curious and difficult tribe of Australian *Rhamneae*" (Hooker 1855, p. 70) and limited the genera to *Pomaderris* (incl. *Trymalium*) and *Cryptandra* (incl. *Spyridium*). He later revised his view in the *Genera Plantarum* (Hooker 1862) and agreed with Bentham (1863) who accepted five genera: *Cryptandra*, *Pomaderris, Spyridium, Stenanthemum* and *Trymalium*.

Ferdinand von Mueller first accepted this view with the exception of Stenanthemum (Mueller 1862). "I was originally inclined to follow J. Hooker in admitting only Pomaderris & Cryptandra amongst the pomaderroid tribe", Mueller wrote to George Bentham on 24 Sep. 1862, continuing that he "finally adopted following your lucid remarks Pomaderris, Trymalium, Spyridium & Cryptandra; but I cannot go further & Stenanthemum must go into Spyridium" (Home et al. 2002, p. 159). In 1862, Mueller regarded Spyridium as belonging to a group, including Cryptandra and Trymalium, that was united by the presence of reniform to cordate anthers and hooded petals, in contrast to Pomaderris which had very oblong, versatile anthers and petals that were not hooded. Mueller's Spyridium also contained Stenanthemum, which only differed, in his opinion, in the presence of a "conspicuously cylindrical" calyx-

			(1101: 0101100100000)		(1101. 1110/10/07
Hooker 1855			_	*	
Reissek 1857 Hooker 1862	-		-	-	
Mueller 1862					
Bentham 1863 Baillon 1875 Rodway 1903	-	-	-	-	-
Mueller 1875	100				
Mueller 1882b, 1889					
Weberbauer 1895 Black 1926, 1952 Suessenguth 1953 Curtis 1956 Conn 1983	-	=	-	-	_
Blackall & Grieve 1956 Canning & Jessop 1986 Barker <i>et al.</i> 1988	=	=			
Barker 1981 Wheeler 1987	-		_		
Rye 1995a, b, 1996 Grieve 1998 Walsh & Udovicic 1999 Thiele & West 2004 Thiele 2006	-	-	-	=	-

Pomaderris Trymalium Spyridium Stenanthemum Cryptandra (incl. Stenodiscus) (incl. Wichuraea)

tube. He did not realise the importance of dehiscent fruitlets and a different position of the disc in defining *Stenanthemum* (Thiele 2007). Mueller wrote: "Disci location et figura affirmationem generum Trymalii Spyridii et Cryptandrae parum adjuvat" (Mueller 1862, p. 85). This statement cannot be supported in the light of current research (Thiele & West 2004; Kellermann et al. 2005; Kellermann 2006; Thiele 2007).

Hooker (1862) and Bentham (1863) also divided the genera of Pomaderreae into two groups. The first was defined by a calyx-tube that was produced above the ovary and disc and it contained *Cryptandra* and *Stenanthemum*. The second group included genera with a calyx-tube that was absent or produced between the ovary and disc, namely *Pomaderris*, *Trymalium* and *Spyridium*. In 1875 Mueller seems to have adopted Bentham and Hooker's view, since he stated: "Genera Trymalium, Spyridium, Stenanthemum et Cryptandra forsan e calycis forma melius disponenda" (Mueller 1875, p. 135). As such, he proposed to include *Trymalium* into *Spyridium*, and *Stenanthemum* into *Cryptandra*, with *Pomaderris* as a third genus. But he never went ahead with publishing the relevant new combinations.

Seven years later, Mueller reverted to his original view from 1862, recognising only *Pomaderris* and *Cryptandra*. This time, he made numerous recombinations so as to include all species of *Trymalium*, *Spyridium*, *Stenanthemum* and *Cryptandra* in a greatly enlarged genus *Cryptandra* (Mueller 1882a, b; 1889, 1896). He defined *Cryptandra sens. lat.* as having anthers "almost broader than long", a calyx tube "extended beyond the fruit" and stamens "usually enclosed by the petals" (Mueller 1888, p. 53).

This extreme opinion was not accepted by subsequent taxonomists. Weberbauer (1895) and Suessenguth (1953) to an even greater extent, followed Bentham and Hooker in their treatments of the Australian Rhamnaceae for the first and second editions of Die natürlichen Pflanzenfamilien. However. neither accepted Stenanthemum. as both included its species within Cryptandra. Weberbauer complained that "the form structures of the flowers and fruits" is given too much emphasis in the definition of the genera of Pomaderreae, the limits of which he described as "rather weak" (Weberbauer 1895, p. 421; translated by Barker et al. 1988). In the 'key to genera', Suessenguth used mostly one

character, the length of the floral tube, to distinguish between the Australian genera of Rhamnaceae. By doing this, he continued a 'tradition' of relying chiefly on this single character of floral morphology, which was taken up in many publications, particularly for the distinction between *Spyridium* and *Cryptandra* (*e.g.*, Rodway 1903; Curtis 1956; Canning & Jessop 1986; Harden 1990). But, as Thiele & West (2004, p. 824) noted after examining these two genera, the hypanthium "varies widely and there is a continuous grade in both genera from species in which the tube is very short or indistinct to species in which it is distinct".

The division of the Australian Rhamnaceae into four main genera was maintained in the following decades and species of *Stenanthemum* usually remained in *Cryptandra* or *Spyridium* (see, e.g., Blackall & Grieve 1956; Barker 1981; Cunningham et al. 1981; Conn 1983; Canning & Jessop 1986; Barker et al. 1988; Wheeler 1987) until Rye (1995a) re-instated the genus. A few authors, such as Baillon (1875), Rodway (1903) and Diels & Pritzl (1904), did accept *Stenanthemum*. Bailey (1899), Maiden & Betche (1902), Stanley & Ross (1986) and Bean (2004) recognised *Stenanthemum scortechinii* (F.Muell.) F.Muell. ex F.M.Bailey; however, this is actually a species of *Spyridium* (Thiele & West 2004).

Fig. 1. Changing generic concepts in the main genera of Pomaderreae from 1855 to 2006. Only major floras and revisions are quoted. An asterisk indicates that *Stenanthemum* was not yet described in 1855.

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The limits of genera in the tribe Pomaderreae have long been problematic, because of the importance of rather cryptic characters and the fact that early botanists did not adequately survey floral characters in the group, but instead relied on gross morphological features, such as the length of the hypanthium tube. A lack of good flowering and fruiting material might have contributed to the issue as well. Important characters include, for instance, the type of bracts and stipules, position and type of disc, indumentum on the ovary roof, the way the fruit and fruitlets dehisce and the kind of disseminule. Some of these were already known by botanists, such as Reissek (1848, 1858) or Mueller (1862) but their full importance was only revealed recently in the publications of Barker (1995; referring also to unpublished work by K.R. Thiele and B.L. Rye), Rye (1995a, b; 1996, 2001), Thiele & West (2004), Kellermann et al. (2005), Thiele (2007) and Kellermann (2006). Thiele & West (2004), Kellermann (2006) and Thiele (2007) also provide lists of diagnostic characters for Cryptandra, Spyridium, Stenanthemum and Trymalium.

Spyridium waterhousei and its generic placement

Spyridium waterhousei is a shrub up to 5 m tall, which occurs along creeklines, sugar gum (Eucalyptus cladocalyx F.Muell.) groves and woodlands. In the protologue, Mueller (1862) emphasised the viscid long linear leaves with revolute margins, and few-flowered terminal cymes consisting of "pedicellate flowers" that have three bracts surrounding the calyx-tube. The long, sticky leaves are certainly characteristic for the species. However, the flowers of *S. waterhousei* do not have true pedicels.

Cryptandra has solitary, sessile flowers that are surrounded by rows of spirally arranged bracts. Flowers in Spyridium are sessile and arranged in cymose inflorescences (Thiele & West 2004). Kellermann (2006, p. 102) reported for Spyridium daltonii (F.Muell.) Kellermann that flowers, which appear to be pedicellate, are better interpreted as "one-flowered unit-inflorescences, since each flower is immediately subtended by 2-3 cymose bracts". Correspondingly, the flowers of S. waterhousei that Mueller (1862) described as 'pedicellate' are reduced one-flowered inflorescences, subtended by cymose bracts; the individual flowers are sessile. As such, the species has a typical Spyridium inflorescence (Thiele & West 2004), except that the number of flowers is reduced. Mueller's 'pedicel' is actually the peduncle of a unit-inflorescence.

Mueller further described *Spyridium waterhousei* as having floral leaves that are covered with a felty indumentum and are slightly wider and shorter than the vegetative leaves, cucullate petals, which contain the anthers, a slightly trilobed undivided style, and fruits with persistent calyx lobes that contain three indehiscent, "crustaceous and chartaceous" fruitlets. Most of these characters are now seen to be typical for *Spyridium*, in particular the presence of floral leaves, which are

unknown in *Cryptandra*. The fruitlets in *Spyridium* waterhousei, however, differ from other species of the genus, since they are not particularly papery, but exhibit a harder, bony texture. The fruitlets are typical for *Spyridium* in respect to the thin crystal layer that covers the outer surface and because they are shed whole and act as the disseminule (Thiele & West 2004).

Other characters that place the species well within *Spyridium* are the strongly undulate disc that is indented away from the bases of the filaments and the stipules, which are fused behind the petiole for up to about half of their length. The stipules are not fused around the base of the petiole, as is characteristic for species of *Cryptandra* (Barker 1995; Thiele & West 2004).

The calyx-tube in *Spyridium waterhousei* extends slightly above the disc; a fact noted by Mueller, who described the flower as being campanulate. However, this was reason enough for Bentham to transfer the species to *Stenanthemum* in 1863². Thiele & West (2004) discussed three closely related species of *Spyridium* that all have a very long hypanthium tube and were for decades included in *Cryptandra*. A similar case is *Spyridium waterhousei*, which was one of the many species Mueller (1882) transferred into his amplified *Cryptandra*. Since then, all publications have referred to it as *Cryptandra waterhousei* (see taxonomic section for references).

Schomburgk (1875), in the first published list of South Australian plants, was the only author who used Bentham's name *Stenanthemum waterhousei*. Despite the fact that Bentham had transferred the species to *Stenanthemum*, Tate continued to follow Mueller (1862) in his first census for South Australia, and an enumeration of plants occurring on Kangaroo Island (Tate 1880, 1883). There do not appear to be any contemporary references to Kuntze's (1891) *Solenandra waterhousei*.

Recent molecular systematic analyses have corroborated the morphological evidence for placing the species in *Spyridium*. Using sequence data from nuclear internal transcribed spacer DNA, Kellermann et al. (2005) showed that this species is nested deep within the genus *Spyridium* in a sub-clade consisting of south-eastern Australian species. The same result was produced with data from the chloroplast *trn*L-F region (Kellermann, Udovicic & Ladiges, unpubl. results). The re-instatement of *Spyridium waterhousei* under its original name is long overdue and resolves 150 years of confusion about its generic affinities.

² The inclusion of Spyridium waterhousei into Stenanthemum weakened Bentham's (1863) concept of the genus, since it was the only species that did not fit the generic description properly. For instance, in the generic description of Stenanthemum, Bentham characterises the fruitets as "opening in 2 valves" (p. 435); but in the description of S. waterhousei he classifies the fruitlets correctly as "indehiseent" (p. 437). Perhaps Stenanthemum as a genus would have been adopted more easily by subsequent botanists, if Bentham had not contradicted his own definition of it.

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Taxonomy

Spyridium waterhousei F.Muell.

Fragm. 3: 83 (Sep. 1862), as 'Sp. Waterhousii'; Tate, Trans. & Proc. Rep. Roy. Soc. South Australia 3: 66 (1880) & 6: 159 (1883). -- Stenanthemum waterhousei (F.Muell.) Benth., Fl. Austral. 1: 436 (1863), as 'St. Waterhousii'; M.R.Schomb., Fl. S. Austral. 37 (1875). - Cryptandra waterhousei (F.Muell.) F.Muell. Syst. Census Austral. Pl. 61 (1882), as 'C. Waterhousii'; Tepper, Trans. & Proc. Rep. Roy. Soc. South Australia 10: 288 (1888); F.Muell., Sec. Syst. Census Austral. Pl. 104 (1889); Tate, Trans. & Proc. Rep. Roy. Soc. South Australia 12: 64-65, 94 (1889); Handb. Fl. Extratrop. S. Austral. 98, 233 (1890); Weberb. in Engl. & Pranti, Nat. Pflanzenfam. III(5): 421 (1895); J.M.Black, Fl. S. Austral. 3: 371 (1926); J.G.Wood, Trans. & Proc. Roy. Soc. South Australia 54: 114, 134 (1930); J.M.Black, Fl. S. Austral. ed. 2, 3: 552 (1952); Suesseng. in Engl. & Prantl, Nat. Pflanzenfam. ed. 2, 20d: 118 (1953); Galbraith, Field Guide Wild Fl. S. Austral. 234 (1977); J.H.Leigh et al., Rare Threat. Austral. Pl. 42 (1981); Jessop, List Vasc. Pl. S. Austral. 76 (1983) & ed. 2, 38 (1984); Canning in Jessop & Toelken, Fl. South Austral. 2: 810 (1986); I.Jackson, Fl. Kangaroo Island 153 (1988); W.R.Elliot & D.L.Jones, Encycl. Austr. Pl. 3: 123 (1989); W.R.Barker in Jessop, J. Adelaide Bot. Gard. 12: 62 (1989); Hnatiuk, Cens. Austr. Vasc. Pl. 542 (1990); W.R.Barker in Jessop, List Vasc. Pl. S. Austral. ed. 4, 55 (1993); W.R.Barker, J. Adelaide Bot. Gard. 16: 20-21 (1995); A.Prescott, Blue Five Petals Kangaroo Island 52 (1995); J.D.Briggs & J.H.Leigh, Rare Threat. Austral. Pl. ed. 2, 161 (1996); W.R.Barker et al., J. Adelaide Bot. Gard. Suppl. 1: 90 (2005). — Solenandra waterhousei (F. Muell) Kuntze, Rev. Gen. Pl. 1: 121 (1891), as 'So. Waterhousii'. — Type citation: "In insula halmaturorum ad basin montium Freestone Range. F. Waterhouse" Lectotype (here designated): Salt lagoon at the north foot of the Freestone Range, [Kangaroo Island, SA, 1861,] F.G. Waterhouse s.n. (MEL 2103248; Fig. 2). Isolecotype: MEL 2263634. Possible isolectotype: Kangaroo Island, [SA, 1861,] F.G. Waterhouse s.n. (K ex herb. Hooker).

Common name. The previous common name of the species was "long-leaved cryptandra" (Canning & Jessop 1986). As this name includes the genus, a new common name is desirable. "Long-leaved spyridium" is suggested as a possible replacement.

Illustrations. J.M. Black, Flora of South Australia, 3: 354, Fig. 161A (1926) & ed. 2, 3: 544, Fig. 702A (1952); D.S. Overton & B.M. Overton, Field notes on Kangaroo Island wildflowers, [10] (1985); E.M. Canning in J.P. Jessop & H.R. Toelken, Flora of South Australia, 2: 809, Fig. 427H (1986); I. Jackson, The flora of Kangaroo Island: from the sketchbooks of Ida Jackson, 152, Fig. 187 (1988); I. Holliday, B.M. Overton & D.S. Overton, Kangaroo Island's native plants, 25 (1994), photograph; W.R. Barker, J. Adelaide Bot. Gard. 16: 21, Fig. 2E (1995), stipules only; A. Prescott, It's blue with five petals: Kangaroo Island field guide, 52, Fig. 3 (1995). All illustrations as 'Cryptandra waterhousii'.

Typification. The lectotype specimen at MEL consists of two flowering branches. It is labelled by Waterhouse with the location and also bears an annotation in Mueller's handwriting: "Differt a Spyrid. vexillifero fruct majoribus, coccis subcrustc (non membr) foliis longioribus, inflorescentia &c.". A second

sheet at MEL has the same locality label written by Waterhouse; it consists of one flowering branch. The specimen from the *Herbarium Hookerianum* (K) has two flowering branches similar to the lectotype and is labelled "*Stenanthemum waterhousii* Kangaroo Island Waterhouse" by Bentham. It would have been examined by him when transferring the species from *Spyridium* to *Stenanthemum* (Bentham 1863) and was most certainly forwarded by Mueller to Bentham.

The 'Freestone Range' mentioned in the protologue and on the specimen labels must refer to Freestone Hill in the north-east of Kangaroo Island. The search for other type material of the species at AD and NSW was unsuccessful.

Note. The correct spelling of the epithet is '*waterhousei*' (Greuter et al. 2000), not '*waterhousii*' as used in the recent editions of the *Flora of South Australia* (Canning & Jessop 1986) and the census of South Australian plants (Barker et al. 2005).

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Fig. 2. Cryptandra waterhousei. Photograph of lectotype (F.G. Waterhouse s.n., MEL 2103248).

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